THE PHENOLOGICAL CLASSIFICATION OF PALAEARCTIC LEPIDOPTERA.

A PRELIMINARY ESSAY.

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My previous articles[1] on the phenology[2] of single-brooded lepidoptera used terms, such as " vernal," " autumnal," " very vernal," etc., which presupposed a phenological classification such as has not yet, to my knowledge, been made. In the present paper a preliminary sketch of such a classification is presented, concluding with the consideration of what use, if any, such a classification may have.

A. Continuously-brooded species.

Types: *Utetheisa pulchella*, L., *Melitaea trivia*, Schiff., *Pieris rapae*, L.

B. Two-brooded species.

1. With two consecutive generations. Type: *Euchloë charlonia*, Donz.
2. With a vernal and an autumnal generation. Type: *Ocneria poenitens*, Stgr.
3. With a partial second generation. Type: *Notodonta ziczac*, L.

C. Single-brooded species.

1. Vernal, with an early tendency. Type: *Dichonia areola*, Esp. (=winter flight in mild climates).
2. Vernal, with little deviation. Type: *Cucullia verbasci*, L.
3. Vernal, with a late tendency. Type: *Malacosoma castrensis*, L. (=summer flight in colder climates).
4. Midsummer. Type: *Pachypasa otus*, Drury.
5. Midsummer, with deviation in both directions: " normally autumnal." Type: *Catocala puerpera*, Giorn. (=summer flight in hot climates, autumnal flight in colder climates).
6. Autumnal, with an early tendency. Type: *Volgarctia spectabilis*, Tausch. (=summer flight in colder climates).
7. Autumnal, with little deviation. Type: *Chondrostega aurivillii*, Pungl.
8. Autumnal, with a late tendency. Type: *Amathes lychnidis*, F. (=winter flight in mild climates).
9. Midwinter. None.

I shall now give further names, to illustrate more completely how a number of well-known species are to be attributed to the above categories and classes, together with some necessary comments. It is not merely considerations of space that prevent me from here trying to classify all the British (or Palaearctic) species; it is that I have neither the time for such a study nor the complete reference library necessary

[1] " Notes on the winter flight, in mild climates, of vernal and autumnal moths," *Ent. Rec.*, 15.xi.38; " The summer flight, in cold climates, of vernal and autumnal lepidoptera," *Ent. Rec*, 15.i.41.

[2] " Phenological " here refers rather to season than hour.

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for it. Readers may, if they please, amuse themselves by fitting into these classes the species not here named.

Category A. (*Continuously-brooded species.*)

Papilio demoleus, L., *Leptidia sinapis*, L., *Colias croceus*, Fourc., *Pyrameis cardui*, L., *Celerio lineata* f. *livornica*, Esp., *U. pulchella*, L., *Agrotis segetum*, Schiff., *Agrotis ypsilon*, L., *Rhyacia saucia*, Hbn., *Tathorhynchus exsiccata*,[3] Led., *Laphygma exigua*, Hbn., *Plusia gamma*, L., *Clytie* genus, *Pandesma anysa*, Guen., *Rhodometra sacraria*, L., *Gymnoscelis pumilata*, Hbn., *Macaria syriacaria*, Stgr.; *Melitaea trivia*, Schiff.; *Papilio machaon*, L., *P. rapae*, L.

In a cold climate it may not be apparent that a species belongs to this category; for instance, judging by its biology in England, one would classify *machaon* under Category B, class 3.

The continuously-brooded category A is largely tropical or subtropical in origin, and many of its species are well-known migrants, migration being the alternative to a diapause as a means of surviving climatic extremes. There seem, however, to be two, or even three classes in the category: (1) purely migratory, to which most belong; (2) capable of aestivating, e.g. *trivia*; and (3) capable of hibernating, e.g. *rapae* and *machaon*; of course, if the climate of the habitat does not require it, none of these modes will be employed. I have, however, hesitated to erect these three classes in my scheme of Category A because we do not know enough yet about the biology of many Category A species in subtropical climates. While it is true that a general tendency to one of the alternatives (migration or diapause) to the exclusion of the other can be remarked, we cannot be sure yet that these alternatives are in all cases mutually exclusive. For instance, a consideration of the biology of *machaon* in Iraq (see also Peile[4]) makes it likely that in this and other cases local migration replaces the summer diapause, the unrelieved desert being recolonized by immigrants from oases each spring when the fresh desert food plant reappears. This may also explain how *ypsilon* and *segetum* survive in Iraq; or they may behave like *trivia* there, and aestivate in an early stage; or perhaps again their subterranean larval habits may even permit a continuous, if retarded, summer development, without an actual summer diapause. Until more is known I prefer to delay the erection of these tentative classes, but observe that the second of them (type: *trivia*) can be distinguished from B 2 by the occurrence of at least two broods before the summer diapause and from B 1 by the possession of an autumnal brood (often, however, less numerous), and that the third of them (type: *rapae*) can be distinguished from Category B by its continuous succession of broods on oasis biotopes in a subtropical climate. Perhaps *sinapis* should accompany *trivia*. The habit of migration in the first class is very probably a comparatively recent development in its evolution.

C. Q. Parsons' interesting record of a *saucia* pupa in winter in Devon (*Ent. Rec.*, January 1941, p. 11) suggests that the reason why many migratory species fail to survive English winters is the inadapt-

[3] In the previous articles I regarded *exsiccata* as a single-brooded species, but this year in Shiraz took it not only in spring but, on marshy ground, again in June; I, therefore, tentatively classify it as shown above.

[4] H. D. Peile: "The Butterflies of Mesopotamia," *Journ. Bomb. N.H.S.*, 1921-22.

ibly short pupal stage which either produces an imago in midwinter, killing it or its progeny above ground, or kills the pupa, which cannot survive a delay induced by cold.

Category B. (*Two-brooded species.*)

1. With two consecutive generations: *Euchloë charlonia*, Donz., *Cerura* genus,[5] *Earias irakana*, Wilts.

2. With a vernal and an autumnal generation: *Lymantria amabilis*, Chr., *Ocneria poenitens*, Stgr., *Acronicta megacephala*, F.[6] *Euxoa conspicua*, Hbn., *Discestra arenaria*, Hamps., *Elaphria bodenheimeri*, Drdt., *Pseudathetis fixseni*, Chr., *Catocala lesbia*, Christ.,[10] *Cidaria salicata*, Hbn., *Dyscia plebejaria*, Ob., *Cornifrons ulceratalis*, Led.

3. With a partial second generation: *N. ziczac*, L., and *Harmodia bicruris*, Hufn.

In cold climates, where the summer diapause is not marked, it may be difficult to distinguish class 1 from class 2 of this category. In milder climates the autumnal brood of class 2 tends to run into the vernal. According to South, *salicata*'s second brood is partial in England; this shows that a colder climate can slow down a species belonging to this category, causing it to omit completely or partially the second generation; we shall observe, in due course, an analogous retarding of the life cycle of some Category C species.

I have bred in captivity a partial second (summer) brood of *bodenheimeri* and *arenaria*; this suggests that the two-broodedness of these, and perhaps other species of the category, is not so fixed specifically as the single-broodedness of Category C, but has been comparatively recently evolved, from Category A, in response to climatic influences (heat and aridity).

Category C. (*Single-brooded species.*)

1. Vernal, with an early tendency: *Cucullia wredowi-judaeorum*, Strand., *Dichonia areola*, Esp., *Antitype chosroes*, Brdt., *Spudaea ruticilla*, Esp., *Theria rupicapraria*, Schiff., *Dasycorsa modesta*, Stgr., *Zamacra flabellaria*, Heeger.

2. Vernal, with little deviation: *Papilio alexanor*, Esp., *Zegris eupheme*, Esp., *Saturnia* genus, *Simyra dentinosa*, Frr., *Monima stabilis*, View., *Cucullia* verbascum- and scrophularia-feeding group, *Lithostege dissocyma*, Prt., *Lithostege palaestinensis*, Ams.

3. Vernal, with a late tendency: *Aporia crataegi*, L., *Melitaea cinxia*, L., *Malacosoma castrenis*, L., *Lacydes semiramis*, Stgr., *Procris* genus, *Phragmataecia castaneae*, *Agrotis elbursica*, Drdt., *Rhyacia nyctimerina*, Stgr.

4. Midsummer: *Leucoma salicis*, L., *Leucoma wiltshirei*, Coll., *Callimorpha quadripunctaria*, Poda, *Pachypasa otus*, Drury., *Stygia saharae*, Luc.

5. Midsummer, with deviations in both directions: "normally autumnal": *Apopestes spectrum*, Esp., *Phragmitiphila typhae*, Thnbg., *Archanara sparganii*, Esp., *A. algae*, Esp.,[7] *A. geminipuncta*,

[5]Seitz, "Die Grossschmetterlinge der Erde," II, p. 283.

[6]I classify two-brooded *Acronicta* under B2 rather than B1 because the Bagdad *Acronicta* (=*aceris*??) clearly belongs there.

[7]I took *A. algae* (=*cannae*) near Shiraz together with *typhae* in mid-June 1941.

Haw., *Mormonia neonympha*, Esp., *Catocala puerpera*, Giorn., *C. promissa*, Esp., *C. optima*, Stgr., and many *C. congener*.

6. Autumnal, with an early tendency: *Volgarctia spectabilis*, Tausch., *Thaumetopoea pityocampa*, Schiff., *Phragmataecia territa*, Stgr., *Agrotis ripae*, Hbn.

7. Autumnal, with little deviation: *Eriogaster* genus, *Lasiocampa*[8] genus, *Chondrostega aurivillii*, Pngl.

8. Autumnal, with a late tendency: *Ocnogyna loewii*, Z., *Rhyacia xanthographa*, Schiff., *Blepharita trisignata*, Men., *Aporophyla australis*, Bsd., *Meganephria oxyacanthae*, L., *Dryobota furva*, Esp., *Dryobotodes roboris*, H.G., *Antitype rufocincta*, Hbn., *A. canescens*, Dup., *Amathes* genus, *Lithostege buxtoni*, Prt, *Larentia clavaria*, Haw., *Cheomatobia brumata*, L., *Itame berytaria*, Stgr., and *Crocallis* genus.

9. Midwinter.

The only difference between classes 1 and 3 of this category is that class 1 is earlier in all climates; similarly, with classes 6 and 8. These four classes thus form a series of similarly-reacting classes spread over the year.

As far as I know, no single-brooded "winter-moth" occurs both before and after the coldest weather in cold climates as *clavaria* does in mild climates; all tend to fly either definitely before or after mid-January. (*Cidaria basochesiata*, Dup., which flies in winter in Mediterranean countries, probably has two broods, and if so can be classed with *salicata* (B 2), which also appears to fly all winter in mild climates.) For this reason, and because cold is a more absolute stopper of insect-life than extreme heat, I think that there can be no true midwinter moth to put in C 9.

In cold climates some species of this category take more than one year over their life-cycle. This may occur in two ways: (a) retarded larval growth; regularly in any given climate (e.g., *Cossus cossus*, L., *P. castaneae*, *L. quercus*, *callunae*); (b) retarded pupal development; irregularly, or individually (e.g. *Eriogaster lanestris*, *T. pityocampa*, etc.). Presumably these two types are due to different causes: type (a) can be explained as simply due to retardment by cold, but one can be less sure of the cause of type (b's) behaviour: since Talhouk's breeding of *Eriogaster philippsi*, Bart.,[9] and my own observations of *Thaumetopoea wilkinsoni*, Tams, and *Eriogaster amygdali*, Wilts., seem to show that in subtropical climates this phenomenon does not occur, I incline to think the phenomenon of irregular pupal delay in type (b) may represent a survival of an ingrained generic habit of pupal aestivation, formed in a subtropical climate and persisting in a distorted form in a cool temperate climate.

My inclusion of the marsh species *typhae*, etc., in class 5 might be taken to indicate that I have changed the view expressed in previous papers that these were "normally autumnal." Phenologically I cannot separate them from the majority of the *Catocala* species, many of

[8]For the remarkable record of a *Lasiocampa* in May at Amara, Iraq, see my paper, "Mesopotamian Desert Lepidoptera," which is being published this year by the *Journal of the Bombay N.H.S.*; the classification of this species (*grandis*, Rog.) may have to be reconsidered when more is known of this phenomenon.

[9]*Ent. Rec.*, 15.vii.40

which are attached to oasis trees. This class is peculiar in not shirking a summer flight in hot climates, though autumnal in colder ones. The seeming paradox can be explained by the availability of its foodplants (tree-foliage or water-plants) even in mid-summer in hot climates, so that acceleration in response to heat is not fatal. On the other hand the absence of a second brood in this class in hot climates, when the foodplant is still available for one, points to the life-cycles having been "fixed" in a cool climate, where, as we see, the class is autumnal. My previously expressed view still seems to hold good.

If some of the above classifications seem arbitrary to any reader, who has not read the previous papers quoted above, I must refer him to them and remind him of the importance of considering the habits of a species over its whole range. Since a cold climate frequently does not give scope to a species' full potentialities, the species must be considered by its behaviour in a more favourable environment.

It may be useful here to define the various types of classification other than phenological, in order to avoid any confusion of thought:— 1. Systematic, by structure. 2. Zoogeographical, by range. 3. Visual, by pattern. 4. Ecological, (a) by foodplant, (b) by habitat (biotope).

The first of these is fundamental, being indispensable in practice and also illuminating the study of phylogenetics, etc. The second touches a subject of a highly speculative nature but of irresistible interest, whose study is still in its infancy. For the value of the third type I advise readers to refer to Cott's *Adaptive Coloration in Animals*, Methuen, London, 1940. Type 4a is chiefly of practical value, and type 4b has, as far as I know, never been thoroughly made by an entomologist, though in my published record of the Lepidoptera of Iraq[10] I tried to record them according to their respective biotope, since Iraqian biotopes are so well defined.

Phenological, a fifth type of classification might be of two kinds, (a) by season, (b) by hour of flight; the former is here attempted.

In conclusion, I may be reminded that although classification is a typical activity of the human mind, it should only be given rein to in useful directions. In case, however, it has not already appeared, from some of the comments made incidentally, that phenological classification is both illuminating and of practical use, I defend it briefly as follows:—

Practical uses: (a) It may help to identify. An example of this use will be found on p. 37 of *South*, Vol. II, where we find these words: "In England we certainly have a *Cucullia* sometimes appearing in the moth state rather later than *verbasci* and always earlier than *C. lychnitis*; the caterpillar producing it feeds on *Scrophularia nodosa* . . . We shall not be greatly opposed to Continental methods if we continue to allow April and May moths resulting from *S. nodosa* caterpillars to do duty for *C. scrophulariae*." I do not necessarily support this identification, but it is an example of how two criteria, i.e., foodplant and season, other than the more usual ones of structure and pattern, are

[10] *C. lesbia* inhabits oases in very hot districts. I have bred it in June and also taken it in November. Further records may perhaps prove it to be consecutively brooded, but I classify it in B2 provisionally. Its phenology is evidently different from that of its congeners, probably representing a more primitive type.

used to determine specimens. To consider the season will often help in other cases of doubt. (b) It may help entomologists to find a species that otherwise eludes them.

Enlightenment: (a) It sheds light on the question of insect migration. (b) It illumines also the central problem of all zoogeographical speculations, i.e., the past history of a species or race—a problem of importance because we can only understand the present status of an insect if we understand its past history. Entomology and geology here overlap, just as, in the human field, geography and history overlap.

A comparison of the phenology of congeneric species is especially interesting in this connection.

Some of the comments made above will have already illustrated how this classification sheds light on that problem; pursuing those comments further, it may be remarked that Categories A and B are closer together than to C, which is distinguished by a more rigid life-cycle, and has presumably evolved in response to the special conditions of the Temperate Zones (Palaearctic and Nearctic). Cold may retard this life-cycle but heat never accelerates it. Freer behaviour and wider reactions are to be observed in Category A. Category B occupies an intermediate position, perhaps exemplifying how Category C evolved from Category A. The tentative classes A 2 and 3 may similarly exemplify the evolution from A 1 to B. In fact, I have tried to classify Categories A and B in order of development, starting with what I consider the more primitive class. It is, however, arguable that B 1 is less primitive than B 2. I should be interested to learn from any reader about the phenology of *castaneae* in tropical climates.

The example of *machaon*, which in England would seem to belong to B 3 but in well-watered warm biotopes is revealed as a member of Category A, like its tropical congener *demoleus*, L. (which only just enters the Palaearctic Zone in the extreme south and there is able to perform a short hibernation in an early stage in climates with a mild winter) affords a good example of how one class or category may evolve from another; suppose, for instance, that *machaon* died out everywhere except in England, then one would definitely classify it as B 3. If the English climate grew colder and it survived, it might perhaps drop its second (partial) brood altogether (it has done so already in Arctic Russia)) thereby entering Category C, in one of the vernal classes. If these climatic conditions were prolonged, this behaviour might become "fixed," so that, if later it extended its range from the cold centre of distribution to warmer climates again, it would remain single-brooded, i.e., it would behave rather as the peak-dwelling *Papilio alexanor* does to-day in the mountains of Syria and Iran. I do not, of course, suggest that all the species of Category C became single-brooded in this way; indeed, on the contrary, I have suggested previously that many became so "fixed" in a centre of distribution with a warm dry summer. But this hypothetical history would explain very well the single-broodedness of C 5, if we substitute "autumnal" for "vernal."

I have assumed above that the evolutionary order was A, B, C because I understand that it is generally accepted that insect life started developing in an age when a hot moist climate was more widespread in the world than now.